

TURNOVER AND DISPERSAL OF PRAIRIE FALCONS IN SOUTHWESTERN IDAHO

ROBERT N. LEHMAN¹ AND KAREN STEENHOF

*USGS Forest and Rangeland Ecosystem Science Center, Snake River Field Station, 970 Lusk Street,
Boise, ID 83706 U.S.A.*

LESLIE B. CARPENTER

Boise State University, Raptor Research Center, Boise ID 83725 U.S.A.

MICHAEL N. KOCHERT

*USGS Forest and Rangeland Ecosystem Science Center, Snake River Field Station, 970 Lusk Street,
Boise, ID 83706 U.S.A.*

ABSTRACT.—We studied Prairie Falcon (*Falco mexicanus*) breeding dispersal, natal dispersal, and turnover at nesting areas in the Snake River Birds of Prey National Conservation Area (NCA) from 1971–95. Of 61 nesting areas where falcons identified one year were known to be present or absent the following year, 57% had a different falcon. This turnover rate was 2–3 times higher than that reported elsewhere for large falcons, and may have been related to high nesting densities in the NCA. Turnover at nesting areas was independent of nesting success in the previous year, but was significantly higher for females nesting on large cliffs. Mean distance between natal and breeding locations for 26 falcons banded as nestlings and later encountered as nesting adults was 8.9 km. Natal dispersal distances were similar for males and females, but more than twice as many males marked as nestlings were later encountered nesting in the NCA. Fourteen adult falcons found on different nesting areas in successive years moved an average of 1.5 km between nesting areas; males dispersed significantly farther than females. Natal and breeding dispersal distances in the NCA were lower than those reported for Prairie Falcons in other study areas. Only four falcons banded as nestlings were found outside NCA boundaries during the breeding period, and only one of these birds was known to be occupying a nesting area. We encountered no falcons banded outside the NCA occupying nesting areas in the NCA during this study.

KEY WORDS: *Prairie Falcon; Falco mexicanus; banding and marking; breeding dispersal; natal dispersal; nest-site fidelity; population turnover.*

Renovación y dispersión de *Falco mexicanus* en el suroeste de Idaho

RESÚMEN.—Estudiamos la dispersión reproductiva, la dispersión natal y la renovación en áreas de anidación en el Area Nacional de Conservación del Snake River (ANC), desde 1971–95. De las 61 áreas de anidación que fueron identificadas en un año y en las cuales los halcones estuvieron presentes o ausentes en el año siguiente, 57% tenían un halcón diferente. Esta tasa de renovación fue 2–3 veces mas alta que la reportada en otros sitios para halcones grandes, y pudo haber estado relacionada con las altas densidades en ANC. La renovación en las áreas de anidación fue independiente del éxito de anidación en el año anterior, pero fue significativamente mayor para las hembras anidando en grandes riscos. La distancia media entre los sitios de reproducción y natalidad para 26 halcones anillados como pichones y posteriormente encontrados como adultos en anidación fue de 8.9 km. Las distancias de la dispersión natal fueron similares para machos y hembras; pero fueron mas del doble en los machos marcados como pichones que fueron encontrados anidando en la ANC. Catorce halcones adultos encontrados en distintas áreas de anidación en años sucesivos se desplazaron un promedio de 1.5 km entre áreas de anidación; los machos se dispersaron significativamente mas lejos que las hembras. Las distancias de la dispersión natal y reproductiva en la ANC fueron mas bajas que las reportadas para estos halcones en otras áreas de estudio. Solo cuatro halcones anillados como pichones fueron encon-

¹ Present address: Dept. of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523 U.S.A.

trados por fuera de los límites de la ANC durante el período reproductivo y tan solo una de estas aves ocupó el área de anidación. No encontramos ningún halcón anillado por fuera de la ANC ocupando algún área de anidación durante este estudio.

[Traducción de César Márquez]

Many raptor nesting areas are occupied year after year, but usually it is not known whether the same individuals occupy the same nesting areas in successive years (Newton 1979). Fidelity to nesting areas varies among species and populations. Small species with short life spans and those that occupy unpredictable environments are less likely to be sedentary than large, long-lived species occupying stable habitats (e.g., James et al. 1989, Jenkins and Jackman 1993, Rosenfield and Bielefeldt 1996). Within populations, older birds, successful breeders, and birds occupying high quality nesting areas often are more faithful to their nesting areas in successive years (Newton 1986, Village 1990, Fore-ro et al. 1999). In most bird species, females move farther from the natal site to breed, change nesting locations more often, and move greater distances between nesting areas used in different years than males (Greenwood 1980, Greenwood and Harvey 1982).

Few data are available on Prairie Falcon (*Falco mexicanus*) turnover and dispersal. Steenhof et al. (1984) reported natal dispersal data for southwest Idaho for the 1970s and early 1980s, and Runde (1987) reported turnover and dispersal data for study areas in Wyoming, Colorado, and Alberta. Since the early 1980s, more than 1000 Prairie Falcons have been marked in the Snake River Birds of Prey National Conservation Area (NCA) in southwest Idaho, providing an opportunity for a more thorough analysis of turnover and dispersal than was possible in 1984. We were particularly interested in whether patterns of dispersal were related to gender, environmental factors, or reproductive success, and whether patterns in the NCA were similar to those in other study areas. We hypothesized that female falcons would exhibit higher turnover rates and disperse farther than males, and that turnover rates would be highest at nesting areas that failed to produce young in the previous year. We also expected turnover rates to be high at nesting areas with low long-term occupancy rates and at those on large cliffs, where potential nest sites were abundant.

STUDY AREA

The NCA comprises 196 225 ha of canyonlands and shrubsteppe desert adjoining the Snake River in south-

western Idaho (USDI 1995). Our study focused on a 130-km stretch of the Snake River Canyon extending from Walters Ferry on the west to Hammett on the east. This area supports the densest known nesting concentration of Prairie Falcons (USDI 1979). During years when full counts of nesting pairs were obtained (1976–78, 1990–94), numbers ranged from 160 to 206 (Steenhof et al. 1999). In parts of the NCA where falcon densities are highest, canyon walls reach 125 m in height and often stretch uninterrupted for many kilometers. In these areas, falcons typically nest <200 m and occasionally <50 m from other pairs (Steenhof 1998). In other parts of the NCA, nesting pairs may be up to 5 km apart. Prairie Falcons leave the NCA soon after young fledge and migrate to widely separated post-nesting and wintering areas, primarily east and south of the NCA (Steenhof et al. 1984).

METHODS

Marking. From 1970–94, 2060 Prairie Falcons were banded in the NCA primarily during two periods of intensive research (USDI 1979, 1996), and as part of annual monitoring efforts (Table 1). All falcons were banded with U.S. Fish and Wildlife Service (FWS) leg bands, and 1189 birds also received colored leg bands, patagial markers (Kochert et al. 1983), and/or radio-transmitters (USDI 1979, Vekasy et al. 1996, Marzluff et al. 1997), depending on research objectives (Table 1). Adults were trapped between March and June each year, and nestlings were banded in May and June, just before fledging. We applied several types of colored leg bands, particularly during the late 1980s and 1990s. Plastic bands were used in 1977 and 1986, and anodized aluminum bands were used in 1987 and from 1990–94. From 1986–94, all color bands were inscribed with a unique alpha-numeric code.

Data Collection. We defined a historical nesting area as any area of cliff where a Prairie Falcon pair was found in one or more years but where no more than one pair nested in the same year (Newton and Marquiss 1982). From 1973–95, we mapped 317 historical nesting areas based on records of 3170 nesting attempts. Delineated areas included scrapes, perches, and defended areas. We defined an encounter as a determination of a bird's FWS band number or alpha-numeric code by any means (Harmata et al. 1999). During most years, data collection was incidental to other research and monitoring efforts (see Steenhof et al. 1999 for methods). However, the intensive field efforts conducted in the late 1970s and early 1990s provided more opportunities to encounter marked birds than in other years. In 1995, efforts to locate and identify marked birds were more systematic. That year, we tried to identify falcons at all nesting areas where falcons had been radiotagged in 1994, by trapping adults or reading band numbers from a distance. If 1994 occupants were not present in their nesting areas in 1995, we searched for them in the two nearest nesting areas (typically the

Table 1. Number of Prairie Falcons marked in the NCA, by year and age class, 1970–94. Columns give the number banded with FWS leg bands. Additional markers (number and type) are given in parentheses (P = patagial tag, R = radiotransmitter, C = colored leg band).

YEAR	NESTLINGS BANDED	ADULTS BANDED	TOTALS
1970	16	0	16
1971	110	0	110
1972	142	0	142
1973	0	0	0
1974	41	0	41
1975	79 (8P, 7R)	3 (3R)	82
1976	151 (107P, 9R)	8 (2P, 6R)	159
1977	118 (10P, 32C)	11 (5C, 4R)	129
1978	104 (74P)	14	118
1979	75 (57P)	0	75
1980	79	0	79
1981	7	0	7
1982	4	0	4
1983	19	0	19
1984	68	0	68
1985	0	0	0
1986	25 (25C)	0	25
1987	104 (91C)	0	104
1988	0	1	1
1989	0	0	0
1990	80	20 (20C, 18R)	100
1991	154 (148C)	29 (28C, 28R)	183
1992	213 (195C, 79R)	34 (33C, 31R)	247
1993	118 (116C, 73R)	49 (42C, 38R)	167
1994	151 (147C)	33 (33C, 32R)	184
Total	1858	202	2060

adjacent upstream and downstream sites). During most years, we used binoculars and 15–60× spotting scopes to observe falcons. From 1991–95, we also used a 160× Questar telescope to read alpha-numeric codes on colored leg bands.

Turnover. We estimated turnover as the proportion of nesting areas occupied in successive years where marked adults identified the first year were not present the following year. We considered that turnover occurred if a different individual was trapped during the second year; if a bird's color band inscription did not match that of the previous occupant; if a bird's band color or placement differed from that of the previous occupant; if the new occupant was unmarked; or if the previous occupant was encountered in another nesting area or was found dead. We used nesting areas more than once in the analysis if the same occupant was identified in more than two consecutive years or if both occupants were marked in the same year. Nesting areas that were vacant the year after birds were marked were not used in the analysis.

To assess factors that might influence turnover, we classified nesting areas according to nesting success in the year before turnover was assessed, long-term occupancy,

and cliff height. We considered a nesting area successful if ≥ 1 young reached 30 d of age (Steenhof 1987). We based occupancy rates on the proportion of years that pairs were present at nesting areas in our sample during 8 yr when full surveys of the NCA were conducted (1976–78, 1990–94) (Steenhof et al. 1999). We classified nesting areas that had pairs present $\leq 65\%$ of years ($N = 10$) as low occupancy sites. Those with pairs present $> 65\%$ of years ($N = 36$) were classified as high occupancy sites. We computed cliff-height categories at nesting scrapes from studies that interpreted aerial photographs using standard parallax methods (Bentley and Hardyman unpubl. data). We considered cliffs ≤ 30.6 m to be small and those > 30.6 m to be large. These categories reflected the fact that most cliffs in the NCA are under 30.6 m in height, but higher cliffs often reach 125 m.

Dispersal. We calculated natal and breeding dispersal distances from Universal Transverse Mercator coordinates assigned to banding and encounter locations. To assess natal dispersal, we recorded all cases where falcons marked as nestlings were encountered later as breeding adults. To assess breeding dispersal, we recorded all cases where breeding adults were encountered in different nesting areas in subsequent years, including birds banded as nestlings if they moved to different nesting areas after we found them breeding. We measured distances between nesting scrapes if known, or between centers of nesting areas if locations of nesting scrapes were unknown. We also counted the number of historical nesting areas between nesting areas used by the same falcon.

Data Analysis. We ran all statistical tests using SAS software (SAS Institute Inc. 1990). Because our investigation was exploratory in nature and our sample sizes were small, we opted to increase power and reduce the risk of Type II errors by considering P -values ≤ 0.10 as significant. We used contingency table analysis (G -tests) to assess gender differences in turnover and in the tendency of falcons to breed near their natal areas. We also used G -tests to relate turnover to nesting success in the previous year, cliff height, and long-term occupancy. Because dispersal data were not normally distributed, we used the Wilcoxon rank sums test, a nonparametric alternative to the t -test, to assess differences in natal and breeding dispersal distances. We identified gender of nestling and adult falcons using foot pad length at the time they were banded (Marzluff et al. 1991) and copulatory behavior observed after release. Birds with foot pads < 86 mm were considered to be males; those with foot pads > 86 mm were considered to be females.

RESULTS

Encounters with Marked Birds. We recorded 76 encounters with 63 marked falcons (34 males and 29 females) at 46 nesting areas during breeding seasons from 1976–95. Sixty-five encounters occurred between 1990–95. Twenty-six (41%) of 63 individuals encountered were marked as nestlings, and 37 (59%) were marked as breeding adults. We recorded more than one encounter with 12 birds: 11 falcons were recorded at nesting areas in two

Table 2. Status and turnover at Prairie Falcon nesting areas in the NCA one year after they were occupied by marked adults, 1975–94.

	NUMBER OF NESTING AREAS				TURNOVER
	SAME BIRD	DIFFERENT BIRD	UNKNOWN OCCUPANT	VACANT	
Males	11	11	51	24	50%
Females	15	24	55	28	61%
Both sexes	26	35	106 ^a	52	57%

^a Includes 4 nesting areas for which occupancy was not confirmed the following year.

different years after they were banded, and one bird was seen in three different years.

Turnover. We evaluated 219 nesting areas where marked adults were known to be present in at least one nesting season from 1970 to 1994. Of these, 102 were occupied the following year by falcons we did not check for identity, 52 were vacant, and occupancy was unconfirmed for 4 (Table 2). This left 61 cases for turnover assessments. Of these, 26 had the same bird and 35 had a different bird the following year. Thus, turnover was 57% for both sexes combined. Turnover was similar for males (50%) and females (61%) ($G_1 = 0.76$, $P = 0.38$).

Of 35 nesting areas where turnover of marked birds occurred, 18 were occupied by new individuals with known band numbers, and 17 were occupied by unidentified birds. In the latter 17 cases, we knew turnover occurred because eight previous occupants were on different nesting areas, six new occupants were unbanded, two new occupants wore different colored bands than those of the previous occupant, and one previous occupant was found dead soon after its first encounter. We were able to account for only one missing bird from the 18 nesting areas where new birds were identified. This bird was found dead near its former nesting area early in the second breeding season.

Sample sizes were inadequate to assess annual turnover for most years. However, in 1995 we confirmed if marked birds had returned to their former nesting areas in 19 cases. Of these, seven nesting areas (37%) were occupied by the same individual, and 12 nesting areas (63%) were occupied by a different bird. This turnover rate (63%) did not differ from that of all other years (55%) ($G_1 = 0.38$, $P = 0.54$).

Turnover of marked falcons was independent of nesting success in the previous year and long-term occupancy of the nesting area. New birds appeared at 4 of 10 nesting areas with low long-term occu-

pancy rates (40%), compared to 31 of 51 nesting areas with high occupancy rates (61%) ($G_1 = 1.46$, $P = 0.30$). Turnover occurred at 19 of 32 successful nesting areas (59%), compared to 10 of 18 unsuccessful nesting areas (56%) ($G_1 = 0.07$, $P = 0.79$).

When we considered relationships between turnover and nesting success in the previous year and turnover and long-term occupancy by sex, we found no differences for males or females ($G_s \leq 2.50$, $P_s \geq 0.11$). However, cliff height was related to female but not male turnover. Only 3 of 14 females returned to nesting areas on large cliffs, compared to 12 of 25 females on small cliffs ($G_1 = 2.80$, $P = 0.09$).

Site Fidelity. At least 26 falcons returned to their former nesting areas the year after they were marked or last seen (Table 2). Of these, two females returned to the same nesting area for a third consecutive year. Both birds occupied their nesting areas from 1977–79. The 26 falcons also included a male that returned to the same nesting area for two consecutive years and one nonconsecutive year. This bird, banded as a nestling in 1990, was found at a nesting area >14.2 km downstream from its natal area in 1991, 1992, and 1994. It likely occupied this same nesting area in 1993, but identification was inconclusive. In 1995, it was replaced by a marked, 1-yr-old male. Five other individuals (3 males and 2 females), not included in the sample of 26 falcons described above, were found in the same nesting areas in two nonconsecutive years.

Natal Dispersal. Of 1858 Prairie Falcons banded as nestlings (Table 1), 26 (1.4%) were encountered during subsequent breeding seasons. These 26 falcons were 1–5-yr old when encountered on nesting areas (Table 3). More than twice as many males ($N = 18$) were encountered as females ($N = 8$) ($G_1 = 2.01$, $P = 0.08$).

Distances between natal areas and breeding sites

Table 3. Natal dispersal distances (km) of Prairie Falcons marked as nestlings between 1972–94 that returned to occupy nesting areas in the NCA as breeders.

AGE IN YEARS	MALES ^a		FEMALES ^b		BOTH SEXES		
	NO. BIRDS	MEAN \pm SD	NO. BIRDS	MEAN \pm SD	NO. BIRDS	MEAN \pm SD	RANGE
1	3	12.3 \pm 8.1	0		3	12.3 \pm 8.1	3.4–19.3
2	6	5.6 \pm 4.4	1	5.8	7	5.6 \pm 4.0	1.1–13.0
3	4	19.0 \pm 14.9	2	8.2 \pm 2.1	6	15.4 \pm 12.8	6.3–35.6
4	4	6.7 \pm 5.0	5	5.6 \pm 2.9	9	6.1 \pm 3.7	1.7–14.1
5	1	8.3	0		1	8.3	
Total	18	10.1 \pm 9.3	8	6.2 \pm 2.6	26	8.9 \pm 8.0	1.1–35.6

^a Range (all males): 1.1–35.6.^b Range (all females): 1.7–9.8.

were similar for males (\bar{x} = 10.1 km; median = 6.35 km; range = 1.1–35.6 km) and females (\bar{x} = 6.2 km; median = 5.9 km; range = 1.7–9.8 km) (S = 98; P = 0.59) (Table 3). Numbers of historical nesting areas between natal and breeding sites for males (\bar{x} = 24.4; range = 2–95) and females (\bar{x} = 19.6; range = 5–44) also were similar (S = 101; P = 0.72). In three cases where we had dispersal data on closely related individuals, distances and direction moved were similar (Table 4).

Four falcons banded as nestlings in the NCA were encountered as yearlings outside the NCA during the breeding season (Steenhof et al. 1984). These birds were encountered in northern Idaho, western Montana (>300 km from the natal areas in both cases), eastern Oregon (101 km from the natal area), and southern Idaho (41–116 km from the natal area). Only the bird in southern Idaho was known to be occupying a nesting area at the time of the encounter; however, it was not identified to individual, so we could not determine the exact distance it dispersed.

Breeding Dispersal. We recorded 20 encounters with marked adults in different nesting areas one or more years after their last known breeding location. None of these encounters occurred outside the NCA. Falcons found one year later (N = 14) moved an average of 1.5 km (Table 5). Males dispersed significantly farther (\bar{x} = 3.3 km; median = 2.75; range = 1.5–6.2 km) than females (\bar{x} = 0.7 km; median = 0.5; range = 0.1–1.9 km) (S = 49, P = 0.009). When we included six falcons (a female and 5 males) encountered two to three years after their last known nesting location, mean distance between nesting areas increased to 2.0 km (Table 5). With movements in nonconsecutive years included, dispersal distances of males were still greater than females (S = 117, P = 0.09).

Of 20 individuals encountered in new nesting areas one or more years after they were last identified, 10 (2 males and 8 females) moved to adjacent nesting areas. The remaining 10 individuals (5 males and 5 females) crossed 1–28 nesting areas (\bar{x} = 7.5) during dispersal movements. Males (\bar{x} =

Table 4. Natal dispersal of related individuals in the NCA. All birds shown were banded as nestlings.

RELATIONSHIP	YEAR BANDED	YEAR ENCOUNTERED	DIRECTION MOVED	DISTANCE MOVED (km)
Brother	1987	1990	Southeast	27.5
Sister	1987	1991	Southwest	1.7
Brother	1990	1991	Northwest	14.2
Brother	1990	1992	Northwest	13.0
Father	1987	1990	Southeast	6.5
Son	1990	1992	Southeast	4.8
Son	1990	1993	Southeast	6.3

Table 5. Breeding dispersal distances (km) for Prairie Falcons that moved from a previous year's nesting area. Sample size is in parentheses.

	SEX	MEAN DISPERSAL	
		DISTANCE \pm SD	DISPERSAL RANGE
Consecutive years	Male	3.3 \pm 2.0 (4)	1.5–6.2
	Female	0.7 \pm 0.6 (10)	0.1–1.9
	Both	1.5 \pm 1.6 (14)	0.1–6.2
All encounters	Male	3.4 \pm 4.5 (9)	0.2–14.4
	Female	0.8 \pm 0.7 (11)	0.1–1.9
	Both	2.0 \pm 3.2 (20)	0.1–14.4

11.0; range = 1–28) and females (\bar{x} = 4.4; range = 1–7) crossed similar numbers of nesting areas during these movements (S = 31.5, P = 0.46).

Of 26 falcons that returned to the same nesting areas in consecutive years, five used the same nesting scrape as the previous year. Of 21 falcons found in the same nesting areas but in different nesting scrapes, 17 moved <0.5 km. The other four falcons moved 0.5–0.8 km. When these falcons were included in estimates of breeding dispersal, mean dispersal distance for encounters in consecutive years dropped to 0.8 km: 1.2 km for males (N = 13), and 0.5 km for females (N = 22).

DISCUSSION

Turnover. Turnover for Prairie Falcons in the NCA was 2–3 times higher than rates reported in other studies of large falcons (Mearns and Newton 1984, Runde 1987, Court et al. 1989). High turnover rates in the NCA may be due partly to high falcon densities. Mean density of nesting pairs throughout the NCA is 0.7 pairs per linear km, and densities reach 4.3 pairs per km in areas where cliffs exceed 100 m in height (Steenhof 1998). Most nesting areas where we studied turnover were in the deepest parts of the canyon; thus, densities in our study area were more than 4 times those reported elsewhere. The highest mean densities recorded for Prairie Falcons in other study areas were 0.6 pairs per km in southwestern Wyoming (Runde 1987), and 0.3 pairs per km on the Kevin Rim, Montana (Harmata et al. 1991). Density may affect turnover by influencing the availability of potential mates. Where densities are low, returning to a previous breeding area may be the most effective means of finding a mate. Where densities are high, abundance of potential mates may reduce a

falcon's need to return to a specific former nesting area.

High turnover in the NCA also may be related to the abundance of nest sites in the area, and the fact that nesting cliffs tend to be continuous. Each year, many historical nesting areas in the NCA are unoccupied. No more than 206 Prairie Falcon pairs have been recorded nesting in the NCA in any given year (Steenhof et al. 1999), yet 317 historical nesting areas have been identified. Where nest sites are abundant and distances between alternate sites are low, frequent moves to different nesting locations might be expected.

Other factors may affect turnover in large falcons, including gender, previous nesting success, long-term occupancy, and nest site or mate quality. The fact that females tended to move more often than males is consistent with studies that suggest turnover in large falcons is slightly higher for females (Runde 1987, Enderson and Craig 1988, Court et al. 1989). In this respect, our data are consistent with overall trends in birds (Greenwood 1980, Greenwood and Harvey 1982). However, our data are inconsistent with other studies in two respects. In Eurasian Sparrowhawks (*Accipiter nisus*) and Eurasian Kestrels (*Falco tinnunculus*), turnover was lower for birds that nested successfully the previous year, and for those from nesting areas with high long-term occupancy rates (Newton 1986, Village 1990). In the NCA, birds from previously successful nesting areas and nesting areas with high long-term occupancy rates showed no greater tendency to return than birds from unsuccessful nesting areas and nesting areas with low long-term occupancy; but females nesting on large cliffs were more likely to move than those on small cliffs. Our results again may be related to the abundance of ledges, cavities, and potential mates in the NCA. Falcons from some previously successful nesting areas may have been displaced by other individuals seeking higher quality sites or better mates, or some falcons may have moved to better nesting areas. The abundance of potential partners and places to nest made it likely that individuals displaced from former nesting areas would find other breeding opportunities.

Dispersal. Both natal and breeding dispersal distances in the NCA were shorter than previously reported for Prairie Falcons (Runde 1987). As in most studies of dispersal, the natal and breeding dispersal distances we recorded may be biased downward because we did not search for marked

birds outside the NCA. Furthermore, our searches for marked birds focused on previously used and adjacent nesting areas. Thus, we were more likely to find birds within a few kilometers of their natal or previous breeding sites. This bias may partly explain why both our natal and breeding dispersal distances were shorter than for Alberta, Colorado, and Wyoming (Runde 1987).

As with turnover, population density and habitat features also could explain shorter dispersal distances in the NCA. Falcons do not need to travel far to find nesting sites or mates in the NCA because stretches of cliff tend to be continuous and potential mates are abundant. In other parts of western North America, nesting cliffs are widely scattered and nesting pairs are clumped, typically with <10 pairs on individual buttes or escarpments (Runde pers. comm., Harmata et al. 1991). Birds that do not return to their natal or former nesting areas have fewer alternative sites available for nesting and fewer mate choices. Those that leave the local area to find breeding opportunities must travel greater distances.

In contrast to Runde's (1987) findings and the predictions of Greenwood (1980) and Greenwood and Harvey (1982), natal dispersal distances for females in the NCA were not longer than males. However, if females dispersed outside the NCA, we would not have found them and recorded the distances. Although our encounter rate likely underestimates the total number of returning birds, it is relatively unbiased with respect to gender because we banded similar numbers of males (923) and females (935) as nestlings and we trapped similar numbers of adult males (90) and females (100) as breeders. Thus, our findings suggest that males were more likely than females to return to breed in the NCA and are consistent with predictions of female-biased dispersal in raptors.

The fact that we encountered few birds marked as nestlings in later years is partly an artifact of our failure to check for birds at all nesting areas, and should not be construed as evidence for frequent emigration. Low encounter rates also may be related to high post-fledging mortality in the NCA (McFadzen and Marzluff 1996). Short natal and breeding dispersal distances, and the fact that only one falcon banded inside the NCA is known to have nested outside NCA boundaries, may indicate that very little dispersal from or into the NCA occurs. However, because many falcons inside the NCA in any given year were unmarked, and be-

cause we conducted no searches for marked falcons outside the NCA, conclusions regarding the extent of falcon immigration into and dispersal from the NCA must remain tentative.

ACKNOWLEDGMENTS

This paper is a contribution of the U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Snake River Field Station (formerly the Raptor Research and Technical Assistance Center). The U.S. Bureau of Land Management (BLM) provided funds from 1972–94 as part of its Snake River Birds of Prey Research Project and the cooperative BLM/Idaho Army National Guard (IDARNG) Project. IDARNG funding was provided primarily through W.S. Seegar, U.S. Army Chemical Research and Engineering Center. The National Biological Service (NBS) and Idaho Power Company provided additional funding and support. A.R. Bammann, J.H. Doremus, T.C. Dunstan, D.L. Evans, J.S. Marks, M.Q. Moritsch, S. Sawby, and G. Sitter played a key role in collecting data in the early years of the study. We thank the Idaho Cooperative Research Unit, M.G. Hornocker, and V.T. Ogden for the 1970–72 banding data, and A.M.A. Holthuijzen for banding falcons in 1987. This paper would not have been possible without the assistance of more than 30 individuals who encountered previously marked falcons. We thank Greenfalk Consultants personnel, especially J.C. Bednarz, J.M. Marzluff, J.O. McKinley, L.S. Schueck, R. Townsend, and M.S. Vekasy, who were responsible for trapping and radiotagging Prairie Falcons and for providing observations of marked birds from 1990–94. We also thank all the BLM, NBS, and Boise State University field technicians who reported observations and assisted in banding young. Special thanks go to J.O. McKinley and R.R. Olendorff, Jr. for 1995 data collection. J.C. Bednarz, J.M. Marzluff, D.E. Runde, J.H. Enderson, and two unidentified reviewers made valuable comments on earlier drafts. Finally, we thank Deana Parrish for data automation.

LITERATURE CITED

- COURT, G.S., D.M. BRADLEY, C.C. GATES, AND D.A. BOAG. 1989. Turnover and recruitment in a tundra population of Peregrine Falcons *Falco peregrinus*. *Ibis* 131:487–496.
- ENDERSON, J.H. AND G.R. CRAIG. 1988. Population turnover in Colorado peregrines. Pages 685–688 in T.J. Cade, J.H. Enderson, C.G. Thelander, and C.M. White [Eds.], *Peregrine Falcon populations: their management and recovery*. The Peregrine Fund, Boise, ID U.S.A.
- FORERO, M.G., J.A. DONAZAR, J. BLAS, AND F. HIRALDO. 1999. Causes and consequences of territory change and breeding dispersal distance in the Black Kite. *Ecology* 80:1298–1310.
- GREENWOOD, P.J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. *Anim. Behav.* 28: 1140–1162.
- AND P.H. HARVEY. 1982. The natal and breeding dispersal of birds. *Ann. Rev. Ecol. Syst.* 13:1–21.

- HARMATA, A., M. RESTANI, B. HATCHER, A. HOUSE, AND S. GRANTHAM. 1991. Impacts of oil and gas developments on raptors associated with Kevin Rim, Montana. Unpubl. rep. U.S. Dep. Inter., Bur. Land Manage., Great Falls, MT U.S.A.
- , G.J. MONTOPOLI, B. OAKLEAF, P.J. HARMATA, AND M. RESTANI. 1999. Movements and survival of Bald Eagles banded in the Greater Yellowstone Ecosystem. *J. Wildl. Manage.* 63:781–793.
- JAMES, P.C., I.G. WARKENTIN, AND L.W. OLIPHANT. 1989. Turnover and dispersal in urban Merlins *Falco columbarius*. *Ibis* 131:426–447.
- JENKINS, J.M. AND R.E. JACKMAN. 1993. Mate and nest site fidelity in a resident population of Bald Eagles. *Condor* 95:1053–1056.
- KOCHERT, M.N., K. STEENHOF, AND M.Q. MORITSCH. 1983. Evaluation of patagial tag markers for raptors and ravens. *Wildl. Soc. Bull.* 11:271–281.
- MARZLUFF, J.M., C. COODY, T.L. MAECHTLE, M. MCFADZEN, T.C. MILES, L.S. SCHUECK, AND M. VEKASY. 1991. Influence of military training on the behavior of raptors in the Snake River Birds of Prey Area, 1991. Pages 37–95 in K. Steenhof [Ed.], Snake River Birds of Prey Area 1991 Annual Report. U.S. Dep. Inter., Bureau of Land Manage., Boise, ID U.S.A.
- , B.A. KIMSEY, L.S. SCHUECK, M.E. MCFADZEN, M.S. VEKASY, AND J.C. BEDNARZ. 1997. The influence of habitat, prey abundance, sex, and breeding success on the ranging behavior of Prairie Falcons. *Condor* 99: 567–584.
- MCFADZEN, M.E. AND J.M. MARZLUFF. 1996. Mortality of Prairie Falcons during the fledging-dependence period. *Condor* 98:791–800.
- MEARNS, R. AND I. NEWTON. 1984. Turnover and dispersal in a Peregrine *Falco peregrinus* population. *Ibis* 126: 347–355.
- NEWTON, I. 1979. Population ecology of raptors. T. & A.D. Poyser, Ltd., Calton, U.K.
- . 1986. The sparrowhawk. T. & A.D. Poyser, Ltd., Calton, U.K.
- AND M. MARQUISS. 1982. Fidelity to breeding area and mate in sparrowhawks *Accipiter nisus*. *J. Anim. Ecol.* 51:327–341.
- ROSENFELD, R.N. AND J. BIELEFELDT. 1996. Lifetime nesting area fidelity in male Cooper's Hawks in Wisconsin. *Condor* 98:165–167.
- RUNDE, D.E. 1987. Population dynamics, habitat use and movement patterns of the Prairie Falcon (*Falco mexicanus*). Ph.D. dissertation, Univ. Wyoming, Laramie, WY U.S.A.
- SAS STATISTICAL INSTITUTE INC. 1990. SAS/STAT user's guide. Vol. 2. Version 6, 4th Ed. SAS Statistical Institute, Cary, NC U.S.A.
- STEENHOF, K. 1987. Assessing raptor reproductive success and productivity. Pages 157–170 in B.A. Giron Pendleton, B.A. Millsap, K.W. Cline, and D.M. Bird [Eds.], Raptor management techniques manual. Natl. Wild. Fed., Washington, DC USA.
- . 1998. Prairie Falcon (*Falco mexicanus*). In A. Poole and F. Gill [Eds.], The birds of North America, No. 346. Academy of Natural Sciences, Philadelphia, PA and the American Ornithologists' Union, Washington, DC U.S.A.
- , M.N. KOCHERT, AND M.Q. MORITSCH. 1984. Dispersal and migration of southwestern Idaho raptors. *J. Field Ornithol.* 55:357–368.
- , M.N. KOCHERT, L.B. CARPENTER, AND R.N. LEHMAN. 1999. Long-term Prairie Falcon population changes in relation to prey abundance, weather, land uses, and habitat conditions. *Condor* 101:28–41.
- U.S. DEPARTMENT OF THE INTERIOR. 1979. Snake River Birds of Prey special research report to the Secretary of the Interior. Bur. Land Manage., Boise, ID U.S.A.
- . 1995. Snake River Birds of Prey National Conservation Area management plan. Bur. Land Manage., Boise, ID U.S.A.
- . 1996. Effects of military training and fire in the Snake River Birds of Prey National Conservation Area. BLM/IDARNG Research Project Final Report. U.S. Geol. Surv., Biol. Res. Div., Snake River Field Station, Boise, ID U.S.A.
- VEKASY, M.S., J.M. MARZLUFF, M.N. KOCHERT, R.N. LEHMAN, AND K. STEENHOF. 1996. Influence of radio transmitters on Prairie Falcons. *J. Field Ornithol.* 67:680–690.
- VILLAGE, A. 1990. The kestrel. T. & A.D. Poyser, Ltd., London, U.K.

Received 3 March 2000; accepted 28 July 2000